

About a series of cylindrical shelled *Granulina* (Marginellidae) from north east Atlantic waters and the taxonomic organisation of the Granulininae

Acerca de una serie de especies del género *Granulina* (Marginellidae) con concha cilíndrica de aguas del Atlántico nororiental y sobre la organización taxonómica de Granulininae

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ABSTRACT

A series of tiny cylindrical shelled *Granulina* are reported as ranging off the North West African coasts, through the recent finding of several phenae. *G. cylindrata* sp. nov. is described from Senegal, the chromatism of its soft parts and the microsculpture of its shell are presented, as well as the variability of its shell morphology. The species is also recorded from the Cape Verde Islands, together with a closely related species quoted as *Granulina* sp. 1. A third cylindrical shelled species is recorded from Lanzarote, Canary Islands, as *Granulina* sp. 2. The relative demographic density of Granulininae is confirmed as being noticeably variable depending on the species. *Granulina cylindrata* sp. nov. and *Granulina* sp. 1 are placed in the same species group and compared to similar species ranging off North West Africa. Various groups are shown to occur in the Granulininae, distinguishable on the basis of shell outlines and macrosculptures. The placement of *Granulina* in Marginellidae is confirmed on the basis of several shell features. A discussion is held about the general issue of supraspecific organisation in the Granulininae, assessing the validity of taxonomic arguments in view of adequate groupings within the considerable morphologic disparity observed.

RESUMEN

Se refiere la existencia de una serie de diminutas *Granulina* de conchas cilíndricas que se han encontrado en recientes hallazgos en las costas del noroeste de África. Se describe *G. cylindrata* spec. nov. de Senegal, y se muestra el cromatismo de sus partes blandas, la morfología de la concha y su variabilidad, y su microescultura. Esta especie también fue recolectada en las Islas de Cabo Verde al mismo tiempo que otra especie próxima que aquí mencionamos como *Granulina* sp. 1. Una tercera especie con concha cilíndrica es referida de Lanzarote, Islas Canarias, como *Granulina* sp.2. Se confirma que la relativa densidad demográfica de las especies de Granulininae es variable dependiendo de cada una de las especies. *Granulina cylindrata* sp. nov. y *Granulina* sp. 1 son situadas en el mismo grupo de especies y comparadas con otras similares existentes en el noroeste de África. Se muestra que varios grupos de especies existen en Granulininae, siendo distinguibles por el perfil de sus conchas y su macroescultura. La posición del género *Granulina* en Marginellidae es confirmada basándonos en aspectos conchiliológicos. Se comenta el

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problema general de la organización supraespecíficas de Granulininae discutiéndose la validez de los argumentos taxonómicos con destino a la agrupación dentro de la amplia disparidad morfológica disponible.

KEY WORDS: Marginellidae, Granulininae, *Granulina*, North East Atlantic, diversity, disparity, shell morphology, new species, species group, supraspecific taxonomy.

PALABRAS CLAVE: Marginellidae, Granulininae, *Granulina*, Atlántico nororiental, diversidad, desigualdad, morfología de la concha, especie nueva, grupos de especies, taxonomía supraespecífica.

INTRODUCTION

The existence of a significant diversity within the genus *Granulina* Jousseaume, 1888 along the Lusitanian Province and into the neighbouring North East Atlantic area was demonstrated by several recent works, mainly through the taxonomic revisions of GOFAS (1992), LA PERNA (1999), SMRIGLIO, GUBBIOLI AND MARIOTTINI (2000) and BOYER (2001). More focused papers dealt also with the morphologic disparity presented in the genus at this simple regional scale (BOYER AND ROLÁN, 1999; BOYER, PELORCE AND HOARAU, 2003).

This paper deals with a set of species distributed from the Canary Islands to Senegal and presenting the same unusual feature, consisting of a cylindrical to subcylindrical shell outline.

The new evidence provided about the great morphological disparity

present within the genus *Granulina* leads us to reassess the validity of the current taxonomic organisation of this genus and of the subfamily Granulininae Coovert and Coovert, 1995.

Abbreviations

MNCN: Museo Nacional de Ciencias Naturales, Madrid

MNHN: Muséum national d'Histoire naturelle, Paris

NNM: Nationaal Natuurhistorisch Museum, Leiden

ERC: Emilio Rolán Collection

FBC: Franck Boyer Collection

ad: adult, juv: juvenile, sh: empty shell,

spm: live collected specimen, fr:

fragment, stn: station, coll: collected,

L: shell length.

SYSTEMATICS

Family MARGINELLIDAE Fleming, 1828

Subfamily GRANULININAE Coovert and Coovert, 1995

Genus *Granulina* Jousseaume, 1888

Type species: *Marginella pygmaea* Issel, 1869, non-Sowerby, 1846 (= *Marginella isseli* Nevill and Nevill, 1875), by monotypy.

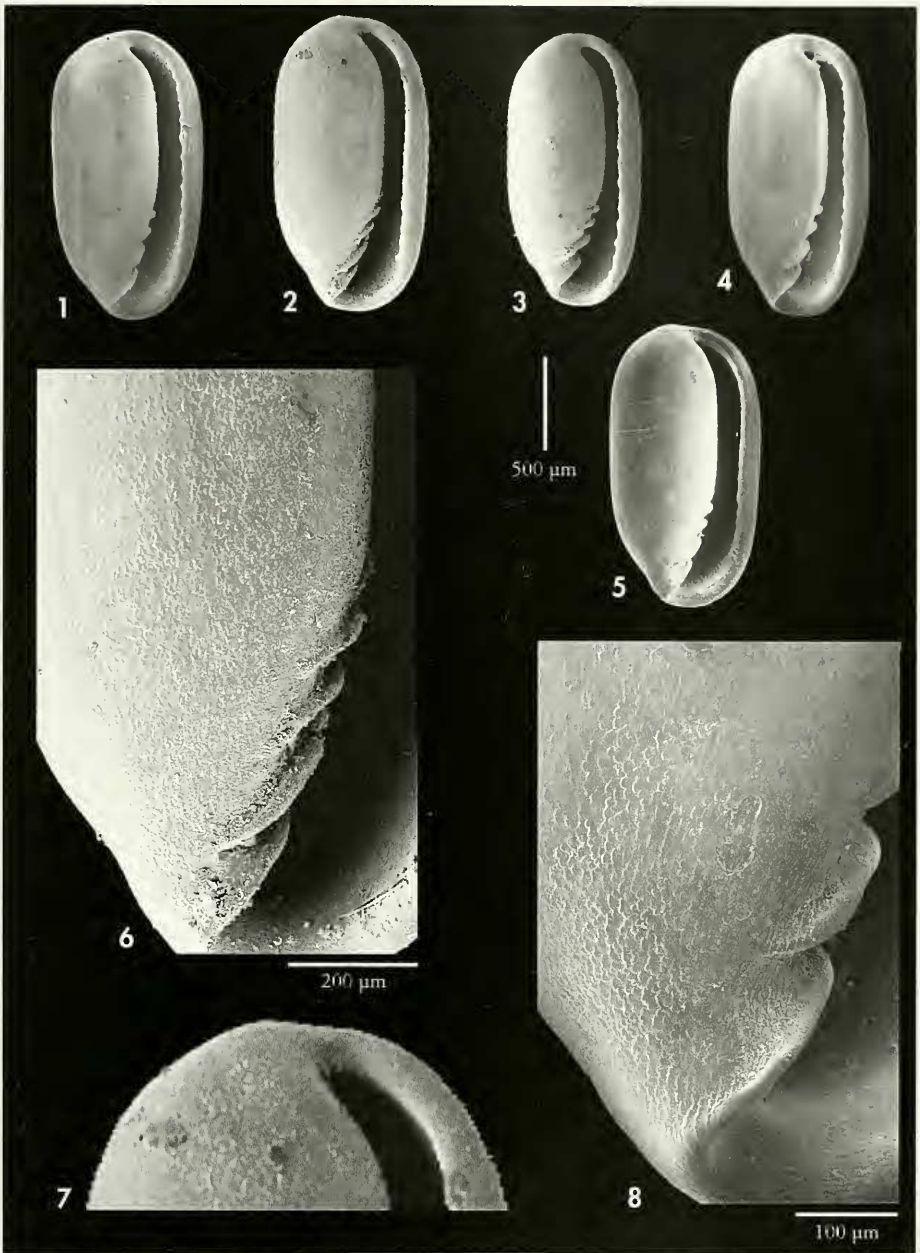
Granulina cylindrata sp. nov. (Figs. 1-11)

Type material: Holotype (Figs. 1, 8), L = 1.58 mm (MNHN). Paratype 1 (Figs. 2, 6-7), L = 1.63 mm (MNCN 15.05/46624); paratype 2 (Fig. 3), L = 1.50 mm, paratype 3 (Fig. 4), L = 1.57 mm, paratype 4, L = 1.30 mm (FBC); paratype 5 (Fig. 5), L = 1.55 mm (ERC). All are empty shells from the type locality.

Type locality: Les Madeleines Islands, off West Dakar, Senegal, 10-18 m.

Other material examined:

From the Dakar area: 1 ad sh, Gorée, 5-6 m (FBC), E. Rolán leg, coll Oct 02. -28 ad and juv sh, M'bao wrecks, 8.5 m (FBC), J. Pelorce leg, coll Sept 98. -2 ad sh and 1 fr, stn Gouye Teni M'bot, 25 m (FBC),



Figures 1-8. *Granulina cylindrata*, Les Madeleines, Dakar. 1: holotype, 1.58 mm (MNHN); 2: paratype 1, 1.63 mm (MNCN); 3: paratype 2, 1.50 mm (FBC); 4: paratype 3, 1.57 mm (FBC); 5: paratype 5, 1.55 mm (ERC); 6-7: same as Fig. 2, paratype 1, details; 8: same as Fig. 1, holotype, detail.

Figuras 1-8. Granulina cylindrata, Les Madeleines, Dakar. 1: holotipo, 1,58 mm (MNHN); 2: paratipo 1, 1,63 mm (MNCN); 3: paratipo 2, 1,50 mm (FBC); 4: paratipo 3, 1,57 mm (FBC); 5: paratipo 5, 1,55 mm (ERC); 6-7: la misma concha que la Fig. 2, paratipo 1, detalle; 8: la misma concha que la Fig. 1, holotipo, detalle.

J. Pelorce leg, coll Sept 98. -1 ad sh, stn Grand Thiouriba, 40 m (FBC), J. Pelorce leg, coll Sept 98. -1 ad spm, 1.50 mm, stn Petit Thiouriba, 38 m (FBC), coll Apr 99.

From the Cape Verde Islands: 1 ad sh, L = 1.60 mm, stn CANCAP VII n° 7.119, off Razo Island, 140 m (NNM), coll 1986.

As *G. cf. cylindrata* form A: 2 ad sh, L = 1.90 mm (Figs. 9, 11), L = 1.70 mm, Les Madeleines, Dakar, 10-18 m (FBC), E. Rolán leg, coll Oct 02.

As *G. cf. cylindrata* form B: 2 ad sh, L = 1.61 mm (Fig. 10), L = 1.50 mm, Les Madeleines, Dakar, 10-18 m (FBC), E. Rolán leg, coll Oct 02.

Etymology: Named from the cylindrical outline of the shell.

Shell description (Holotype, Figs. 1, 8): Dirty white, slender cylindrical outline. Spire absorbed, anterior and posterior tips rounded, left side of the anterior part slightly depressed, aperture moderately open along its posterior $\frac{2}{3}$ and widening considerably along its anterior $\frac{1}{3}$, middle part of the inner labrum straight and vertical, 17 spaced out labial denticles, outer margin thickened. Four protuberant columellar plaits on the anterior $\frac{1}{3}$ of the left border, the second one being the largest, no parietal varix. Microsculpture of the body whorl consists of very fine low granulations covering the whole surface without any special order or orientation.

Dimensions: 1.58 × 0.85 mm.

Radula: Unknown.

Distribution: Known from the vicinity of Dakar, Senegal, numerous shells (6 to 40 m) and one live collected specimen (38 m); Also from Razo Island, Cape Verde Islands, one shell (140 m).

Habitat: The single specimen collected alive (Petit Thiouriba, Dakar, 38 m) was obtained by washing a chitinous clump of chaetopter vermes in a bowl of sea water. It must be noted that most of the fauna found in this special habitat was also found in other kinds of habitat, and the shells obtained by brushing wrecks in the Bay of Gorée seem to come from short algae and moss on hard bottoms.

Remarks: The external features of the soft parts have been studied from a non-type specimen. Foot narrow, truncated ahead and tapering backward, translucent white with a few small yellowish marks on the front part and a narrow central yellowish stripe on the metapodium. Head translucent white, eyes black, a few tiny yellowish marks

on the tentacles, siphon mottled, yellowish. Inner mantle whitish, with a black mark at the centre of the anterior part, crossed by a transversal light-blue mark. Seen by transparency through the shell, the dorsal zone of the siphonal canal shows some axial golden lirations. Outer mantle whitish, with moderate to protuberant white pustules and scattered orange dots.

The single specimen observed in live condition presented a light yellow shell, as did the well-preserved shell from Razo Island, Cape Verde Islands. Many of the shells examined from Senegal in this study present a dirty white to light yellow ground, so it is assumed that the normal colour ground of the shell of *G. cylindrata* sp. nov. is light yellowish. This is a very original feature in the genus *Granulina* and in the subfamily Granulininae, as all the Granulininae known so far have translucent white to opaque ivory shells.

The shell morphology of *G. cylindrata* does not show great variability. In the holotype (Figs. 1, 8) and in paratype 2 (Fig. 3), the top of the shell is perfectly rounded, making a regular arch, whereas the other paratypes show a more or less visible false-spire. All the other features seem very constant, including the shape and the position of the columellar plaits. (Nb. the more transversal appearance of the plaits in paratype 1 (Figs. 2, 6) comes from the orientation of the shell in the photography, with the top of the shell raised towards the lens of the camera). The length of the shells ranges from 1.30 mm to 1.63 mm.

A few shells, collected sympatrically with *G. cylindrata* off Dakar, show somewhat divergent features from those of *G. cylindrata*, without evident intergrades.

Some shells, provisionally named as *G. cf. cylindrata* form A (Figs. 9, 11), can show a larger size ($L = 1.70$ to 1.90 mm), a more oval outline, a slightly more rostrated top and a slight break of the external outline of the labrum, but they remain perfectly coherent with the other specific features of *G. cylindrata*, including the columellar plaits, the morphology of the inner labrum and the microsculpture of the last whorl (compare Fig. 8 and Fig. 11).

Other shells, provisionally named as *G. cf. cylindrata* form B (Fig. 10), present a more divergent morphology. Their outline is very oval, the length ranges from 1.50 to 1.61 mm, the outer lip is very thickened in its middle and posterior part, making a strong low rostrum, the aperture is much narrowed in its median part, a thick callus encompasses the anal canal, a parietal varix bordered by a fine sulcus may be present (Fig. 10, but not in the other shell examined), the 2 lower columellar plaits run parallel in an oblique orientation.

Some of these features might be accepted as gerontic stages of shell growth in *G. cylindrata*, but some others (like the centrally widened labrum, the wide rostrum and the oblique lower plaits) suggest that we are dealing with

a different species, close to *G. crassa* Smriglio, Gubbioli and Mariottini, 2000 described from Western Sahara. However, *G. crassa* is larger ($L = 1.90$ mm), more egg-shaped, its columellar plaits are less protuberant and the second plait is shorter.

Even if *G. cf. cylindrata* form A and form B seem to be specifically distinct from *G. cylindrata*, the determination of their specific identity requires the study of further dead and live material, including a better knowledge of the general variability occurring in *G. cylindrata*.

At infralittoral levels off Dakar, *G. cylindrata* is found in the vicinity of *G. liliputana* (von Maltzan, 1884) and of *G. pierrepineai* Pin and Boyer, 1995 (possible junior synonym of *G. mauretana* Gofas, 1992). In the waters of the Cape Verde Islands (observations in NNM collections and data in BOYER AND ROLÁN, 1999), *G. cylindrata* is sympatric with *G. ocarina* Fernandes, 1987 (possible senior synonym of *G. mauretana* and of *G. pierrepineai*), *G. fernandesi* Boyer and Rolán, 1999 and *G. sp. 1*, which is described below. *G. cylindrata* is easily distinguished from the sympatric species, except the one described below, by its slender cylindrical outline.

Granulina sp. 1 (Figs. 12-14)

Material examined: 1 ad sh (Figs. 12-14), $L = 1.28$ mm, Palmeira, Sal, Cape Verde Islands, 50 m (ERC).

Shell description (Figs. 12-14): Whitish, narrow, cylindrical outline. Spire absorbed, anterior tip rounded, posterior part of the labrum arched, towering above the posterior top of the last whorl, aperture moderately opened, median part of the inner labrum straight and faintly denticulate, outer margin thickened. Three columellar plaits on the anterior $\frac{1}{4}$ of the left border, the anterior one being faintly arched, long and thin, and separated from the two other, which are closely set together. The second one is rather short and more arched, and the third is very short and

transversal, extended by a strong columellar varix running all along the left border of the aperture. Microsculpture of the body whorl damaged, mostly erased.

Dimensions: 1.28×0.69 mm.

Animal: Unknown.

Radula: Unknown.

Distribution: Only known from the upper circalittoral (50 m) of Sal, Cape Verde Islands.

Habitat: Unknown.

Remarks: The shells of *Granulina* sp. 1 differ from those of *G. cylindrata* principally by the more elevated posterior

part of the labrum, the original shape and insertion of its 3 columellar plaits and the presence of a long and strong columellar varix. The shell of *G. fernandesi*, found at upper levels in the same station, is stouter, more inflated and less cylindrical than the one of *G. sp. 1*, it

bears 4 columellar plaits and its inner lip is smooth.

No shell of *G. sp. 1* was found in the samplings made by the CANCAP expeditions (NNM) at circalittoral and lower infralittoral levels from the Cape Verde Islands.

Granulina sp. 2 (Figs. 15-17)

Material examined: 1 ad sh (Figs. 15-17), L = 2 mm, Porto Moro, Lanzarote, 40 m (F. Swinnen coll.), sp1 08-01.

Shell description (Figs. 15-17): Whitish, slender subcylindrical outline, slightly egg-shaped. Spire absorbed, anterior part attenuated, anterior top rounded, posterior tip of the last whorl showing a varix angle, posterior top of the labrum slightly arched and faintly elevated, aperture moderately open, middle part of the inner labrum straight and smooth, outline of the labrum showing a break at its $\frac{1}{3}$ posterior part, outer margin wide and thickened. Four very oblique columellar plaits running along 40% of the left border, the anterior one being the largest, thin and arched, the second one being shorter, thicker and partially unfolded by a faint longitudinal depression, and the 2 posterior ones being small and subequal. A thick columellar varix begins above the upper plait and disappears into a wide columellar callus which spreads along the upper half of the left border and covers the top of the last whorl. Microsculpture of the last whorl damaged, mostly erased.

Dimensions: 2.00 x 1.03 mm.

Animal: Unknown.

Radula: Unknown.

Distribution: Only known from the lower infralittoral of Lanzarote, Canary Islands.

Habitat: Unknown.

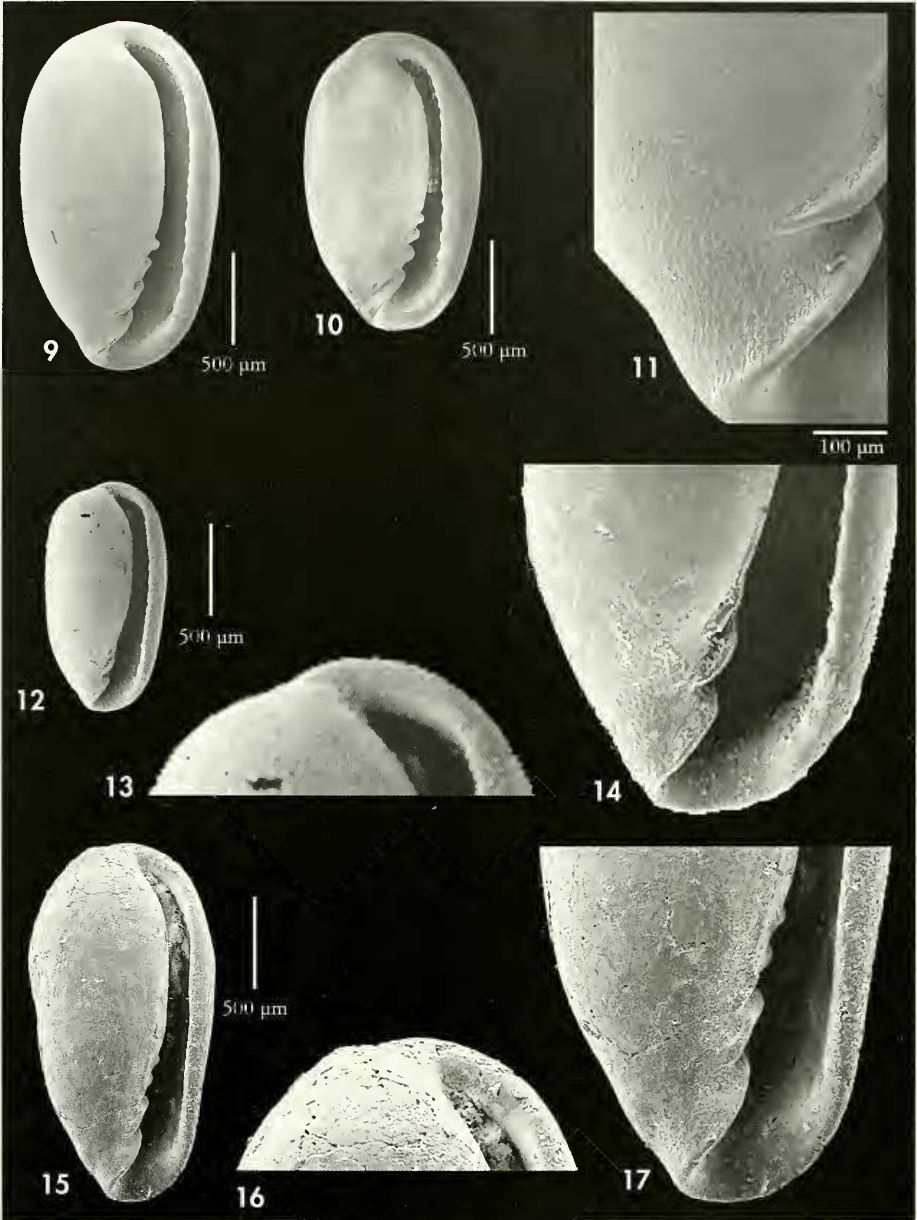
Remarks: The shell of *Granulina* sp. 2 is very similar to those of some species of *Plesiocystiscus* Coover and Coover, 1995. Its partially unfolded second columellar plait and its well-defined outer margin are however clear diagnostic

features allowing placement in *Granulina*.

Granulina sp. 2 differs from *G. cylindrata* and from *G. sp. 1* by its slender outline, its attenuated anterior part, its oblique and spaced out columellar plaits, its smooth labrum with a distinct break of the outline. Despite the important difference in features with *G. cylindrata* and *G. sp. 1*, *G. sp. 2* is provisionally placed in the same group on the basis of its general outline. As a matter of fact, it can be considered as closer to this group than to the slender shelled species attributed to the group of *G. occulta* Monterosato, 1869 (see in GOFAS, 1992 and in BOYER, 2001). It must be noted that *G. fernandesi* from the Cape Verde Islands, despite its smaller size and its squat shape, presents some similarities with *G. sp. 2*, with a smooth inner labrum and comparable columellar plaits.

Despite the important microshell material examined from the NNM collections (CANCAP expeditions, mainly from the circalittoral levels of Fuerteventura) and in the private collections of W. Engl, J.M. Hernandez and F. Swinnen (mainly from infralittoral and / or circalittoral levels from Hierro, Gran Canaria and Lanzarote), *G. sp. 2* is only known from the single shell studied above.

Only 3 other *Granulina*, *G. guancha* d'Orbigny, 1840, *G. canariensis* Boyer, 2001 and *G. cf. occulta* are recorded from the waters of the Canary Islands (BOYER, 2001).



Figures 9-11. *Granulina* cf. *cylindrata*. 9 : form A, Les Madeleines, Dakar, 1.90 mm (FBC). 10: *Granulina* cf. *cylindrata* form B, Les Madeleines, Dakar, 1.61 mm (ERC); 11: same as Fig. 9, detail. Figures 12-14: *Granulina* sp. 1, Palmeira, Sal, Cape Verde Islands, 1.28 mm (ERC). Figures 15-17: *Granulina* sp. 2, Porto Moro, Lanzarote, Canary Islands, 2.00 mm (F. Swinnen coll.).
 Figuras 9-11. *Granulina* cf. *cylindrata*. 9 : forma A, Les Madeleines, Dakar, 1,90 mm (FBC) ; 10, 11: *Granulina* cf. *cylindrata* forma B, Les Madeleines, Dakar, 1,61 mm (ERC). 11: la misma concha que la Fig. 9, detalle. Figuras 12-14: *Granulina* sp. 1, Palmeira, Sal, Islas de Cabo Verde, 1,28 mm (ERC) Figuras 15-17: *Granulina* sp. 2, Porto Moro, Lanzarote, Islas Canarias, 2,00 mm (F. Swinnen coll.).

DISCUSSION

Relative demographic density of *Granulina* species: The discovery of *G.* sp. 1 and *G.* sp. 2 as single specimens (despite the significant samplings of microshells performed in the Cape Verde and Canary Islands) and the finding of *G. cylindrata* in limited numbers in a few stations from Dakar (compared to the relative abundance of *G. liliputana* and of *G. pierrepineaui*) corroborates the remark of BOYER (2001) about the occurrence of sparse populations and limited numbers of individuals in some species of *Granulina*, side by side with regularly distributed populations of numerous individuals in other species.

Placement of *Granulina*: The placement of the genus *Granulina* in the family Cystiscidae Stimpson, 1865 by COOVERT AND COOVERT (1995) was contested by LA PERNA (1999), who maintained *Granulina* in the family Marginellidae Fleming, 1828, on the basis of the external morphology of the animal (type 2 animal, *sensu* COOVERT, 1987). This argument is however considered here as unsuitable, due to the fact that the genus *Plesiocystiscus* Covert and Covert, 1995, also placed by COOVERT AND COOVERT (1995) in the subfamily Granulininae, presents a type 2 animal, as well, despite the presence of a triserial radula and of a cystiscid shell. In the present state of knowledge, the external morphology of the animal cannot be considered a reliable diagnostic feature allowing by itself assignation to the Marginellidae (uniserial modified rachiglossan radulae). However, we propose to maintain the genus *Granulina* in the Marginellidae on the basis of a new argumentation dealing with major shell features, such as a thick external margin, a fully developed internal coiling of the columellar plaits (schematically illustrated but apparently interpreted the wrong way by COOVERT AND COOVERT, 1995: 47-51 and fig. 4) and the occurrence of macrosculpture in some species (see BOYER AND ROLÁN, 1999 and SMRIGLIO AND MARIOTTINI, 2001).

Granulina being the type genus of the Granulininae, its conservation by LA PERNA (1999) in the Marginellidae led implicitly to remove the Granulininae from the Cystiscidae to the Marginellidae.

Grouping in the Granulininae: The present report of a set of species with cylindrical shells without macrosculpture tends to confirm preceding ideas concerning both the high specific diversity and the great morphologic disparity occurring in *Granulina* in the North East Atlantic waters. Besides the present report also confirms the occurrence of well-characterized species groups of phyletic origin requiring a more discriminating taxonomic organisation of the Granulininae at the supraspecific level.

In the present state of knowledge, *G. cylindrata* and *G.* sp. 1 are considered as belonging to the same species group, whereas the relationship of *G. fernandesi* and *G.* sp. 2 are considered with more hesitation. Among other things, it must be noted that the microsculpture pattern found in *G. fernandesi* (see BOYER AND ROLÁN, 1999) looks very different to the one found in *G. cylindrata* (Fig. 8). This feature remains undocumented for *G.* sp. 1 and for *G.* sp. 2. *G.* cf. *cylindrata* form A presents the general features shared by the *G. cylindrata* species group, but *G.* cf. *cylindrata* form B presents more divergent features and may belong to a different species group.

The *G. cylindrata* species group looks very different to the "cylindrical" or "square" forms of Granulininae from other areas, like the Caribbean species *Marginellopsis serrei* Bavay, 1911 or the Indo-Pacific *G. atomella* (Bavay, 1917) from the Mascarene Islands, *Pugnus parvus* Hedley, 1896 from the South West Pacific and *Pugnus maesae* Roth, 1972 from Cocos-Keeling. The "cylindrical" or "square" outlines seem to be only convergent features and not to explain a common phyletic origin for all these species. At least 3 different species groups of "cylindrical shelled" Granulininae (respectively represented by *Pugnus parvus*, *Marginellopsis serrei* and *Granulina*

cylindrata) seem to deserve mention at the supraspecific level (for *Pugnus parvus*, see BOYER, 2003, figs 9, 12, 16; for *Marginellopsis serrei*, see BOYER AND ROLÁN, 1999, figs 14-17). The first two of these groups are characterized by original patterns of macrosculptures and the third one by the lack of macrosculpture, whereas the other shell features, besides the general outline, seem to be significant only at the specific level. That is the case, among others, for the number of columellar plaits (for instance in *G. cylindrata* = 4 plaits versus *G. sp. 1* = 3 plaits, or in *P. parvus* = 3 plaits versus *P. maesae* = 4 plaits) or the presence of labial denticles (present for instance in *P. maesae* but lacking in *P. pugnus*).

As far as shell morphology is concerned, the unity of the *Pugnus* group sensu stricto (= *P. parvus* and *P. maesae*) is simply based on the cylindrical outline associated to a heavy spiral macrosculpture (see BOYER, 2003). This granular spiral macrosculpture has nothing to do with the lattice-patterned macrosculpture together with finely granulated microsculpture found in *Marginellopsis serrei* (see in BOYER AND ROLÁN, 1999), whereas the fine smooth spiral macrosculpture of low cords found in *G. atomella* seems a very different pattern, despite a general shell outline intergrading between those of *Pugnus* and of *Marginellopsis*. As far as the different macrosculptures prevailing in the morphs studied are concerned, the synonymy proposed by COOVERT AND COOVERT (1995) between *Pugnus* and *Marginellopsis* cannot be considered acceptable, and the different "cylindrical shelled" species groups of Granulininae cannot be interpreted as constituting a monophyletic set.

Elements about the supraspecific organisation of the Granulininae: The morphologic disparity within the Granulininae was underlined by BOYER AND ROLÁN (1999) and demonstrated in further ways by SMRIGLIO AND MARIOTTINI (2001), BOYER, PELORCE AND HOARAU (2003) and BOYER (2003). The taxonomic interpretation of this disparity however remains controversial.

The subfamily status of the Granulininae is well-supported by the noticeable degree of divergence to other groups of Marginellidae. On the other hand, the wide disparity observed within the Granulininae seems to result from a considerable phyletic radiation that requires a parallel and diversified taxonomic organisation at the supraspecific level. From this point of view, the present taxonomic organisation of the Granulininae can be considered sketchy and rudimentary.

In his revision, GOFAS (1992) used the genus *Granulina* as a single undifferentiated group, possessing its own original features among the Marginellidae and not requiring taxonomic subdivisions at the supraspecific level. When creating the subfamily Granulininae, COOVERT AND COOVERT (1995) divided into two genera, *Granulina* Jousseaume, 1888 (type species: *Marginella isseli* Nevill and Nevill, 1875 from the Red Sea) and *Pugnus* Hedley, 1896 (type species: *Pugnus parvus* Hedley, 1896 from South East Australia), this last one being considered as a senior synonym of *Marginellopsis* Bavay, 1911.

BOYER AND ROLÁN (1999) recorded the occurrence of diversified micro and macrosculptures on the shells of the Granulininae and suggested their use as a diagnostic character in taxonomic and phyletic analysis, besides other characters currently used. These shell sculptures were noted to be original and constant in each species, even in the type species of *Granulina*, *G. isseli* Nevill and Nevill, 1875 from the Red Sea, which shows faint "leopard-patterned" microsculptures on a smooth ground. The possible recognition of several distinctive species groups on the basis of their micro and macrosculpture patterns was advocated, but a better knowledge of the great morphologic disparity widespread throughout the genus *Granulina sensu lato* and a deeper study of its distinctive features was said to be a precondition for taxonomic reorganisation.

SMRIGLIO AND MARIOTTINI (2001) described their new genus *Paolaura* (Granulininae) mainly on the basis of the macrosculpture represented in their type

species *P. semistriata* Smriglio and Mariottini, 2001 from Kenya. This macrosculpture is made of strong spiral cords running on the upper and lower quarters of the last whorl, but lacking in the smooth central part and also at both tips of the shell where a conspicuous microsculpture made of thick disorganised "waves" is to be seen. This microsculpture reaches the aperture and covers also the top of the spiral cords, the irregular spacings being more or less hatched by coarse axial smudges.

Two other species were described in the same genus. *P. kenyanensis* Smriglio and Mariottini, 2001, also from Kenya, shows a shell morphology and sculpture very similar to the one of *P. semistriata*. *P. maldivensis* Smriglio and Mariottini, 2001, from Maldives Islands, presents a noticeably different shell morphology, but almost the same kind of micro and macrosculptures present in *P. kenyaensis*.

BOYER (2003) underlined that if the diagnostic value attached to shell sculpture in the Granulininae is practically demonstrated at the specific level, its value at the generic level remains to be established. For instance, the creation of the genus *Paolaura* was thought to be for poorly argued from the point of view of the morphologic disparity found in the Granulininae. As far as shell morphology is concerned, the best affinities of *P. semistriata* were proposed to be with the South West Pacific species *G. ellicensis* (Hedley, 1899) and *G. hedleyi* Boyer, 2003, better than with *P. maldivensis*. Further study of the variability of shell morphology in *P. kenyaensis* and comparison of the soft parts chromatism will allow us to verify if this phena is really distinct from *P. semistriata*. The same kind of study will allow us to verify whether *P. maldivensis* really belongs to the same phyletic set than *P. semistriata* or if its shell sculpture is only the result of morphologic convergence.

This point deals with good appreciation of "character hierarchy" and with good determination of derived features versus ancestral ones, that is to say with the pertinent reconstitution of phyletic radiations at work. From this point of

view, the question of the clades limits is of basic importance: each diagnostic character used must be defined on the basis of its variability range and must contain an explanation of its own limits, for the simple reason that a too flexible category (or a too rigid one) may have no explanatory value from the point of view of evolutionary biology. In the case of genus *Paolaura*, the possible relationship with *Pugnus* must be tested, considering aspects like a similar kind of spiral macrosculpture and the existence of possible intergrades, such as *G. atomella* which, besides a somewhat square shell outline in most specimens, generally shows a macrosculpture of spaced spiral cords at both tips of the shell and a smooth central part. More generally, a thoughtful well thought out taxonomic organisation of the Granulininae presupposes the identification of those features most subject to modification and those that are more stable within the group, and to verify in particular whether or not the different patterns of shell sculpture are representative of phyletic groups within the Granulininae.

Significantly, the genera distinguished within the Granulininae subsequently to the creation of the genus *Granulina* are all based on a shell morphology characterized by macrosculpture, suggesting that the Granulininae which have no macrosculpture could be joined together in the genus *Granulina*, which is based on a species bearing only shell microsculpture (BOYER AND ROLÁN, 1999). In fact, the Granulininae seem to contain, besides sub-sets of species with macrosculpture such as *Pugnus*, *Marginalloopsis* or *Paolaura*, numerous other sub-sets without macrosculpture, possibly definable as genera on the basis of various kinds of affinity characters. It must be underlined that the phyletic meaning of macrosculpture and its systematic value at the supraspecific level is not documented, and it must be envisaged, in the present state, that any phyletic species group may contain species with macrosculpture and species without macrosculpture.

An advanced work about the organisation of the Granulininae certainly requires the preliminary definition of a genus *Granulina sensu stricto* based on the type species *G. isseli* from Red Sea, which could be related to some Indo-Pacific species such as *G. mariei* (Crosse, 1867) from New Caledonia (BOYER, 2003).

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